A new species of the luvarid fish genus †*Avitoluvarus* (Acanthuroidei: Perciformes) from the Eocene of the Caucasus in southwest Russia

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Abstract.—A new species of the luvarid fish genus †*Avitoluvarus, A. eocaenicus,* is described from the middle Eocene of Russia (Kuma Horizon, North Caucasus) based on a single imprint of its skeleton (incomplete posteriorly). *Avitoluvarus* previously has been known only from the terminal (uppermost) Paleocene of Turkmenistan, where it is represented by two species, *A. dianae* and *A. mariannae.*

The fossil luvarid genus *Avitoluvarus* was described recently (Bannikov & Tyler 1995) from the Danata Formation in Turkmenistan, where it is represented by two species, *A. dianae* Bannikov & Tyler, 1995, and *A. mariannae* Bannikov & Tyler, 1995. The exact age of the fish-bearing layer of the Danata Formation in Turkmenistan has been questioned, with the fishes from this layer dated as both Late Paleocene (Danilchenko 1968, Bannikov 1985) and Early Eocene (Tyler & Bannikov 1992b, Patterson 1993, Bannikov & Tyler 1995). We accept here the analysis of Muzylev (1994) indicating that the fish-bearing layer of the Danata Formation is synchronous with the Upper Thanetian sapropel of more western regions, corresponding to global Late Paleocene anoxic events.

In 1999, excavations in the North Caucasus by the first listed author yielded the imprint of a skeleton (incomplete posteriorly) that represents a new species of *Avitoluvarus*. This specimen was found in the bituminous marls of the Kuma Horizon in the Gorny Luch locality (Pshekha River, Apsheronsk District, about 0.5 km from the Gorny Luch farmstead). The Kuma Horizon correlates with the Bartonian stage. The Kuma Horizon previously has been as-

signed to the Upper Eocene (Tyler & Bannikov 1992a, Bannikov 1993) but according to Cavelier & Pomerol (1986) only the Priabonian (but not the Bartonian) should be included in the Upper Eocene, and thus the Kuma Horizon fishes are of late Middle Eocene age.

A preliminary, and far from complete, list of Kuma fishes (Bannikov & Parin 1997) includes at least 27 species representing 25 families in 10 orders. Based on the recent excavations in 1999, this list can be extended by a number of taxa representing their first discoveries at the generic and familial levels at the Gorny Luch locality; e.g., a champsodontid, an *Antigonia*-like caproid, a *Seriola*-like carangid, a *Sarda*-like scombrid, a percoid fish probably belonging to a new genus of uncertain family, and the new species of luvarid described below. The great majority of the teleost species from the Gorny Luch assemblage are oceanic pelagic (epi- and meso-) and the new species of *Avitoluvarus* described below is presumably epipelagic like the only Recent representative of the family, *Luvarus imperialis* Rafinesque, 1810.

The new species represents the first record of the genus *Avitoluvarus* outside of Turkmenistan and extends the stratigraphic

distribution of this genus from the Late Pa-leocene to the end of the Middle Eocene.

Family Luvaridae Gill, 1885
Genus *Avitoluvarus* Bannikov & Tyler, 1995
Avitoluvarus eocaenicus, new species
Figs. 1–3

Material.—Holotype, Paleontological In-stitute (PIN), Moscow, no. 4425/32, esti-mated 38 mm SL, imprint of poorly pre-served skeleton, incomplete posteriorly, single plate, and counterpart of the head and cleithrum.

Type locality and horizon.—Left bank of Pshekha River, about 0.5 km from the Gor-ny Luch farmstead, Apsheronsk District, Krasnodar Region; Kuma Horizon, upper part of the Middle Eocene.

Etymology.—For the Eocene age of the new species.

Diagnosis.—*Avitoluvarus eocaenicus* has all the available characters (those of the caudal peduncle are unknown because of the incompleteness posteriorly of the holo-type) diagnostic of the genus *Avitoluvarus* (see diagnosis in Bannikov & Tyler 1995: 6). *Avitoluvarus eocaenicus* differs from both of the other two species of the genus, *A. dianae* and *A. mariannae,* by the anter-oventral inclination of the third to fifth hae-mal spines, versus these spines being ori-ented relatively vertically in *A. dianae* and inclined posteroventrally in *A. mariannae* (for comparative data on the two previously described species, here and following, see Bannikov & Tyler 1995). Additionally, *A. eocaenicus* differs from the other two spe-cies by a combination character: the haemal spines of the first two caudal vertebrae are slender and make contact with one another in their middle regions, versus these haemal spines being slender but not contacting one another in *A. mariannae,* or relatively stout and contacting one another in *A. dianae.* These diagnostic haemal spine characters do not change appreciably ontogenetically within the size ranges known for the other

two species of *Avitoluvarus,* and the single specimen of *A. eocaenicus* (38 mm SL) is within the size range of the specimens of *A. mariannae* (34–190 mm SL) and *A. eocaenicus* (38–120 mm SL).

Description.—The holotype of *Avitolu-varus eocaenicus* is probably a juvenile based on the presence of ridges on the skull bones and serrations on the dorsal- and pel-vic-fin spines. Such ridges and serrations are present in other small juvenile (less than about 50 mm SL) luvarids (e.g., as in *A. mariannae* and *Luvarus imperialis*) but these are lost at larger sizes. Also, the skel-eton of *A. eocaenicus* seems to be about as weakly ossified as in *A. mariannae* and somewhat less well ossified than in *A. di-anae.*

The body is fusiform, and its greatest depth is about 41% SL. The head is rela-tively long, about 35% SL. The upper head profile is gently curved and the mouth is small (gap equal to about orbit diameter or less). The round orbit is situated in the low-er part of the upper half of the head and has a horizontal diameter of about 23% of head length.

Skull: The limits of the individual bones of the weakly ossified occipital and otic re-gions are not clear, but the frontals seem to be relatively wide and the supraoccipital lacks a prominent crest. The bones of the cranial roof (probably of the frontals) have remnants of larval ridges, and we presume that these ridges were serrate as in other acanthuroids even though we cannot be ab-solutely sure of this because of poor pres-ervation of the single specimen; one ridge is along the dorsal midline and another, shorter one, is anterior to the orbit.

The ethmoid region is exceptionally weakly ossified. The parasphenoid is slen-der and slightly convex where it is exposed at the lower edge of the orbit. The shaft of the hyomandibular is oriented anteroven-trally. The pterygoid bones and the palatine are unclear. The quadrate is broad, trian-gular, and has a small articular facet for the lower jaw. The symplectic is an elongate

Fig. 1. *Avitoluvarus eocaenicus,* new species, photograph of the holotype, PIN 4425/32, estimated 38 mm SL (incomplete posteriorly), wet with alcohol to improve contrast, Middle Eocene of North Caucasus (Kuma Horizon), Russia. Scale bar is 10 mm.

rod, somewhat stouter posteriorly than anteriorly. There is a faint remnant of a structure in the ethmoid region above the anterior part of the parasphenoid that can be interpreted as a long slender process or prong of the lachrymal similar to that of juvenile specimens of *Luvarus imperialis* (see Tyler et al. 1989).

The lower jaw articulation is situated well in front of the level of the anterior edge of the orbit. The lower jaw is rather short but deep, with the dentary and articular of about equal size. The dentary bears a single row of small conical teeth. The alveolar process of the premaxilla is slender, elongate, and bears a single row of small conical teeth, whereas the ascending process is short but prominent. The maxilla seems to be relatively wide.

The thin, flat bones of the opercular region are poorly preserved, with the limits of the individual bones unclear. The opercle appears to be subtriangular and has several bony ridges radiating from the condylar region. The preopercle is curved along its anterior border, with an angle of about 100°.

Several radiating ridges appear to be present in the upper part of the preopercle.

The hyoid and branchial arches are not clear, but there are five sabre-like branchiostegal rays.

Pectoral fin and girdle: The posttemporal is slender and elongate; it extends from the posterodorsal aspect of the head ventrally and slightly posteriorly. A short intercalar process extends anteriorly from the lower part of the posttemporal. The supracleithrum is elongate and tapered anterodorsally; this bone is disarticulated in the present specimen. The large cleithrum has a gently curved c-shape, with the upper and lower ends inclined, respectively, slightly anterodorsally and anteroventrally. The upper limits of the postcleithrum are poorly preserved, but the long shaft of the bone below the pectoral-fin base is sturdy and reaches ventrally below the ventral edge of the anterior extension of the first anal-fin pterygiophore (this extension is probably displaced postmortem somewhat dorsally) or almost to the ventral margin of the body. There is no evidence of a division of the
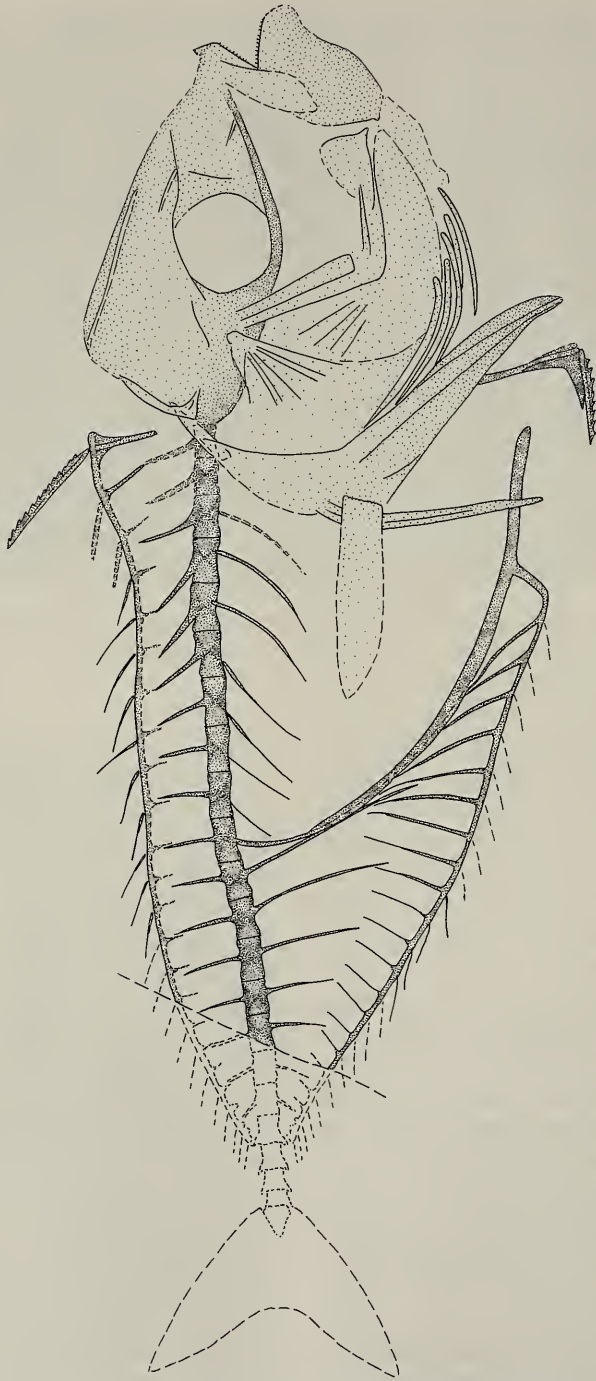
Fig. 2. *Avitoluvarus eocaenicus,* new species, reconstruction of the holotype (for data see legend for Fig. 1). The unstippled parts of the skeleton posterior to the dashed fracture line through the sixth caudal vertebra are missing and hypothesized here as having the conditions of all other species of the family Luvaridae (e.g., a total of 13 caudal vertebrae, the pterygial truss extending posteriorly to the ninth caudal vertebra, four vertebrae in the caudal peduncle, and a forked caudal fin deeply overlapping the hypural plate).

long postcleithral shaft into two pieces, and we presume that the postcleithrum is a single bone (the right and left postcleithra are preserved close alongside one another, except where they overlap ventrally, and are so shown in the reconstruction). The coracoid is elongate, of decreasing width anteroventrally.

The base of the pectoral fin is situated in the middle of the body, slightly above the middle of the distance between the vertebral column and the ventral profile. The pectoral fin is poorly preserved and its length and number of rays cannot be determined.

Pelvic fin and girdle: The pelvis is L-shaped. The long ascending (pubic) process is oriented slightly posterodorsally toward the cleithrum. The posterior (ishial) process is well developed, reaching almost to the level of the anterior end of the anterior extension of the first anal-fin pterygiophore. The posterior process is tapered and shorter than the ascending process. There is essentially no anterior (iliac) process.

The pelvic spine is relatively long (longer than the posterior process of the pelvis), about 8% SL, robust, and bears serrations along its anterior edge, being similar to the first dorsal-fin spine except somewhat shorter. No soft rays are evident in the pelvic fin. The pelvic fin of luvaroids becomes rudimentary with increasing specimen size, or it is absent (Bannikov & Tyler 1995:33), so it can be anticipated that when larger specimens of *A. eocaenicus* become available the pelvic-fin spines will be much shorter (or absent) than in the present specimen of ca. 38 mm SL.

Vertebral column: There are probably 9 + 13 = 22 vertebrae, as in all other species of both fossil and Recent luvarids; if so, the posterior seven vertebrae are missing in the only specimen of *A. eocaenicus* (the missing vertebrae are indicated hypothetically by dashed lines in the reconstruction, Fig. 2). The first two abdominal vertebrae are obscured, but can be reasonably estimated on the basis of the space available for them between the rear of the skull and the front of the centrum that is the first to be clearly exposed (presumably the third abdominal vertebra). The vertebral column is elevated anteriorly and articulates relatively high on the rear of the cranium. All of the preserved centra are somewhat elongate anteroposteriorly. All of the preserved neural spines are short, slender, and only slightly curved. Most of the neural spines are inclined posteriorly, but the orientation of those of the last abdominal and first two caudal vertebrae is close to vertical. The neural spines of the first five caudal vertebrae are shorter than the corresponding haemal spines. The abdominal vertebrae lack parapophyses. Short and slender ribs (pleurals) are present on the third to ninth abdominal vertebrae, becoming slightly shorter posteriorly. The ribs are inclined posteroventrally and reach to a level less than one-half the distance between the vertebral column and the ventral profile of the body. Epineurals are not evident.

The haemal spine of the first caudal vertebra is only slightly thicker than that of the second caudal vertebra; it is only moderately curved anteroventrally in its lower region. The first haemal spine is so closely articulated along its anterior edge to the first anal-fin pterygiophore that its full length cannot be determined. The haemal spine of the second caudal vertebra is very slender and almost straight. The second haemal spine is angled anteriorly from its base at the centrum and closely approaches or contacts the posterior edge of the middle of the first haemal spine, distal to which point of contact these two haemal spines diverge. The haemal spines of the third to sixth caudal vertebrae are exceptionally slender, straight or only slightly curved, and of decreasing length posteriorly in the series. The third to fifth haemal spines are inclined anteroventrally, whereas the sixth haemal spine is oriented slightly posteroventrally, and close to vertical.

The caudal peduncle, caudal skeleton, and caudal fin are missing.

Dorsal and anal fins: The posterior parts of these fins are missing and the total number of dorsal- and anal-fin elements cannot be determined exactly. However, based on the assumption that the missing parts of the dorsal fin are similar to those of other luvarids, we estimate that there are about 24 dorsal-fin elements. The first dorsal-fin element is definitely a spine. It is relatively long, about 11% SL, borne in supernumerary association on the first dorsal-fin pterygiophore, and bears serrations along its anterior edge. The second and third elements are represented by faint remnants; these are evidently thicker than the subsequent elements, and therefore are probably spines. The remaining elements are clearly soft rays that are unsegmented, unbranched, and bilaterally paired (as seen in some elements that are separated into slightly displaced left and right halves). The rays are much shorter than the first dorsal-fin spine. The dorsal-fin pterygiophores are very poorly preserved and the majority of their ventral shafts are unclear. The distal expansions of the dorsal-fin pterygiophores apparently form a continuous truss, but we cannot determine its thickness. The upper region of the ventral shaft of the first dorsal-fin pterygiophore is expanded into lamellar plates both anteriorly and posteriorly. Based on its position, the lower region of the ventral shaft of the first dorsal-fin pterygiophore is situated in what we estimate to be the preneural space in front of the distal end of the neural spine of the first vertebra.

Only a few of the anal-fin rays are preserved, in about the middle of the fin, but based on the number of pterygiophores preserved and of missing parts being similar to those of other luvarids, we estimate that there are about 22 anal-fin rays. The anal-fin rays are unsegmented, unbranched, and bilaterally paired, similar to those of the dorsal fin and of about the same length. The anal-fin pterygiophores are mostly T-shaped in lateral view, with a dorsally oriented shaft and an anteroposteriorly expanded distal end. The first anal-fin pterygiophore has a long, thick anterior extension beneath most of the abdominal cavity, and a long, equally stout posterodorsal process whose upper end firmly articulates along the anterior edge of the lower end of the haemal spine of the first caudal vertebra. The second and more posterior anal-fin pterygiophores have the distal ends expanded into shallow anterior and posterior processes that form a continuous truss that we presume must have been extensively interdigitated even though we cannot determine the details of this because of poor preservation.

As preserved, the ventral edge of the truss in the abdominal region just behind the anterior extension of the first anal-fin pterygiophore is strongly convex (Figs. 1, 2), uniquely so among luvarids. However, we do not believe that this is an autapomorphy of the new species, but, rather, a postmortem artifact associated with the upward displacement of the anterior extension of the first anal-fin pterygiophore above the level of the lower end of the postcleithrum; the weak ossification in this juvenile specimen would lend itself to this distortion. In Figure 3 we show this region of the truss as preserved (A) and as we believe it would appear if undistorted (B).

With the exception of the first anal-fin pterygiophore, the other pterygiophores are very slender. The shafts of the second to sixth pterygiophores are situated between the haemal spines of the first and second caudal vertebrae (first interhaemal space), and those of the seventh to ninth pterygiophores are in the second interhaemal space. The succeeding three interhaemal spaces accommodate two or three pterygiophore shafts each. The shafts of the anal-fin pterygiophores are not especially convergent toward the haemal spines.

Scales: Tiny scales cover the entire body, but poor preservation precludes detailed description.

Discussion

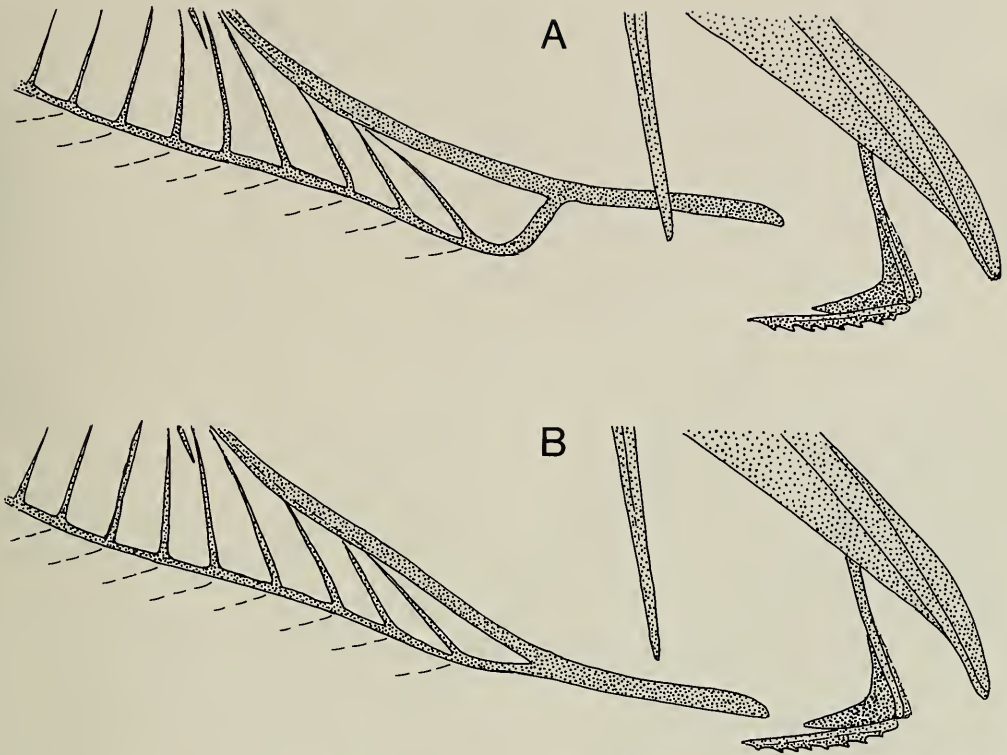Bannikov & Tyler (1995) proposed nine unequivocal synapomorphies for the super-

Fig. 3. *Avitoluvarus eocaenicus,* new species: A, structure of the anterior pterygiophores of the anal fin as preserved with postulated convex distortion of the lower edge of the first pterygiophore in the region behind the anterior process, and with upward displacement of the anterior process above the level of the ventral end of the postcleithrum; B, our interpretation of how the anterior pterygiophores of the anal-fin would appear if undistorted.

family Luvaroidea (Luvaridae + †Kushlu-kiidae) and six unequivocal synapomor-phies for the family Luvaridae (with two species of Paleocene *Avitoluvarus,* and two species of *Luvarus,* one Paleocene and one Recent; Tyler et al. 1989, previously doc-umented a far larger number of synapo-morphies for the Luvaridae based only on the single Recent species, but many of these features cannot be determined in fossils or are unique to the Recent species). Within the Luvaridae, the preponderance of de-rived features were found in *Luvarus,* whereas *Avitoluvarus* was shown to possess only two unequivocal synapomorphies: (1) the truss formed by the interdigitation of the distal regions of the dorsal- and anal-fin pterygiophores is relatively shallow and not extensively interdigitated; and (2) the prox-imal shafts of a total of seven to 11 (rarely six) anal-fin pterygiophores are situated in the first two interhaemal spaces (here and following, character numbers are in paren-theses and correspond to those in the clad-ogram, Fig. 4).

Within *Avitoluvarus,* Bannikov & Tyler (1995) identified one autapomorphy of *A. dianae* as (3) the posterodorsally oriented proximal shaft of the first anal-fin ptery-giophore is especially thick and stout, and three autapomorphies of *a. mariannae* as: (4) the proximal shafts of a total of 10 to 11 anal-fin pterygiophores are situated in the first two interhaemal spaces (the greater increase in number of pterygiophores in these two spaces in *A. mariannae* being a more derived condition than the lesser in-crease in *A. dianae*); (5) the ribs are rela-
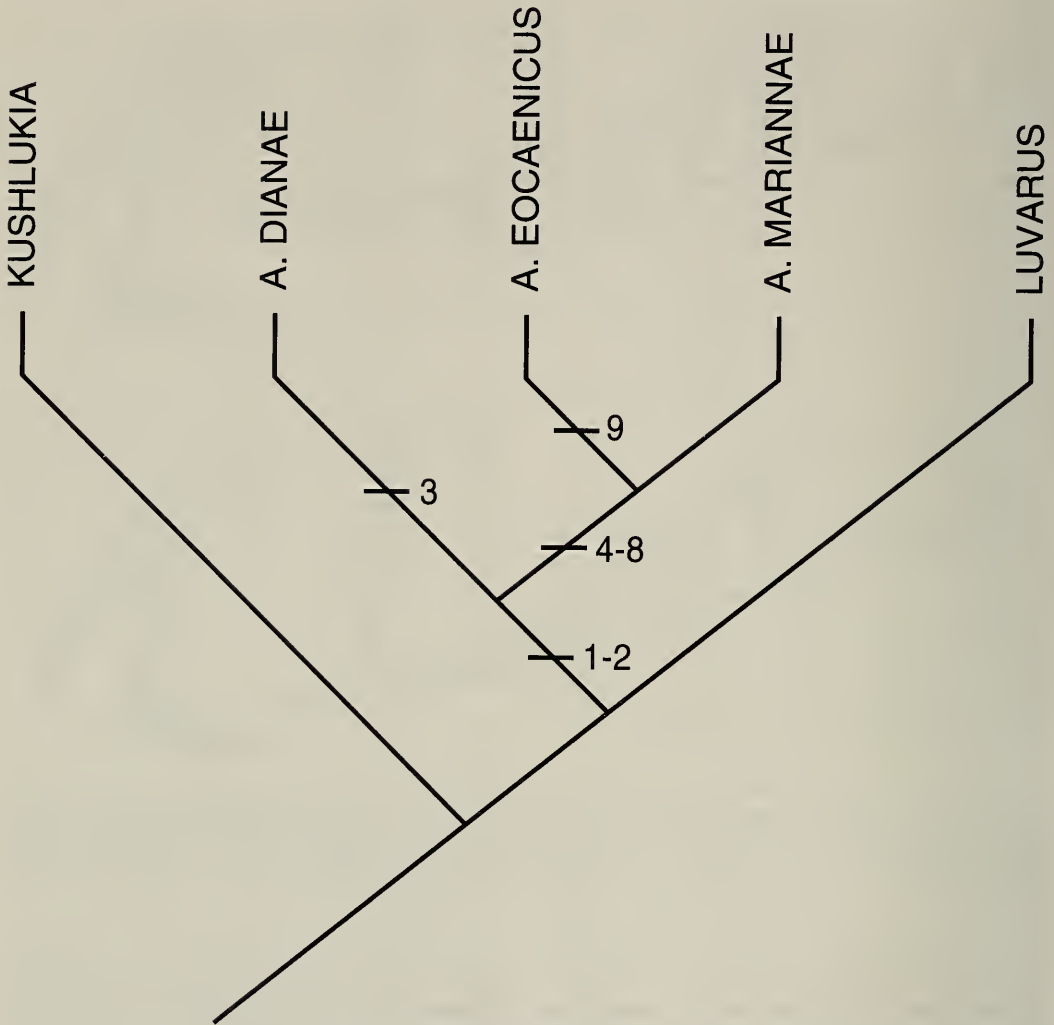
Fig. 4.   Cladogram of the proposed relationships within *Avitoluvarus*. Derived character states, discussed in the text, are: (1) pterygial truss shallow and not extensively interdigitated; (2) proximal shafts of a total of 7–11 (rarely 6) anal-fin pterygiophores situated in the first two interhaemal spaces; (3) posterodorsally oriented proximal shaft of the first anal-fin pterygiophore especially thick and stout; (4) proximal shafts of a total of 10–11 anal-fin pterygiophores situated in the first two interhaemal spaces (5) ribs relatively short and thin, ending at the level of the upper third of the abdominal cavity; (6) ventral half of pterygial truss especially shallow; (7) first two haemal spines only slightly thickened; (8) proximal shafts of the second and many of the more posterior anal-fin pterygiophores exceptionally slender; (9) third to fifth haemal spines inclined anteroventrally. Character states 1–6 and 9 are unequivocal apomorphies, but states 7–8 are equivocal and apomorphic only under the assumption of delayed transformation, favoring independent acquisition over reversal. For data supporting this and the sister group relationships of *Kushlukia* with *Avitoluvarus+Luvarus,* see Bannikov & Tyler (1995).

tively short and thin, ending at the level of about the upper third of the abdominal cavity; and (6) the ventral half of the pterygial truss formed from the distal ends of the anal-fin pterygiophores is very shallow.

Moreover, *A. mariannae* was shown to possess two equivocal autapomorphies (which assume delayed transformation, favoring independent acquisition over reversal, with the ancestor possessing the plesiomorphic

condition of the outgroups): (7) the first two haemal spines are only slightly thickened; and (8) the proximal shafts of the second and more posterior anal-fin pterygiophores, except for the last few, are exceptionally slender.

The new species, *A. eocaenicus*, shares four derived character states (5–6 unequivocal, 7–8 equivocal) with *A. mariannae* and lacks the single autapomorphy (3) of *A. dianae*, all of which indicates a sister group relationship between *A. eocaenicus* and *A. mariannae*.

For one character (4), *A. eocaenicus* is intermediate between *A. dianae* and *A. mariannae*. Two to five anal-fin pterygiophore shafts in the first two interhaemal spaces is ancestral for acanthuroids (Bannikov & Tyler 1995), and the increase in number of such pterygiophores in *Avitoluvarus* can be considered an ordered transformation series of increasing specialization from the six to seven in *A. dianae* to the eight in *A. eocaenicus*, to the 10–11 in *A. mariannae*. For this character within *Avitoluvarus*, we consider the eight or more pterygiophores in these two spaces as a derived condition synapomorphic for *A. dianae* and *A. mariannae*.

We identify an autapomorphy of *A. eocaenicus* as (9) the third to fifth haemal spines are inclined anteroventrally. We consider posteroventral to vertical inclination of the third to fifth haemal spines as ancestral for acanthuroids because this is the condition found in fossil and Recent scatophagids (the first outgroup for acanthuroids), siganids, zanclids, and most acanthurids (including those considered to be the most basal): see illustrations in Tyler et al. 1989, Blot & Tyler 1991, Tyler & Bannikov 1997, Tyler & Sorbini 1999). Among the luvarid + †kushlukiid clade (Bannikov & Tyler 1995), anteroventral orientation of the third to fifth haemal spines is found only in one of the two species of *Kushlukia* (in *K. permira*, versus posteroventral orientation in *K. sp.*), in one of the two species of *Luvarus* (in *L. imperialis*, versus vertical to posteroventral in *L. necopinatus*), and in

one of the three species of *Avitoluvarus* (in *A. eocaenicus*, versus posteroventral in *A. mariannae* and vertical in *A. dianae*). It is most parsimonious to propose that the anteroventral orientation has arisen independently in the single species of *Kushlukia, Luvarus,* and *Avitoluvarus;* therefore, the anteroventral orientation of the third to fifth haemal spines is an autapomorphy of *A. eocaenicus*.

Conclusion

The addition of another new species to the record of fossil luvarids reinforces the notion (Bannikov & Tyler 1995:40) that the luvaroid fishes were far more diversified in the early Tertiary (six species in two families, with four species from the uppermost Paleocene of the Danata Formation, Turkmenistan, alone) than they are today, when only a single species survives.

Acknowledgments

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